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INTRODUCTION

In connection with genetic and taxonomic studies of *Crepis*, an examination of as many species as could be brought into cultivation has been in progress for about ten years. The earlier work on the chromosomes was done by Dr. Margaret Mann Lesley, who studied particularly numbers and sizes (Mann, 1922, 1925; Babcock and Lesley, 1926). The work of M. Navashin (1925, 1926) and Taylor (1925, 1926), who described satellites and constrictions for the first time in this genus, showed that a closer morphological study of the chromosomes from suitably fixed material would be of value for comparative studies of related species.

It is the purpose of this paper to present our knowledge of number and morphology of the chromosomes in seventy species and to consider this evidence in relation to a system of classification based on phylogenetic relationship. But the present paper is not intended to serve as a taxonomic treatise. Therefore no keys or descriptions of species will appear and there will be no attempt to set forth the detailed evidence for the phylogenetic groupings proposed, as such descriptions and data will appear in a taxonomic treatment now in preparation. The specific names used have been carefully verified as to identity, priority, and authorship, and are in nearly every case the same as those which will be used in later publications. In the present paper it is proposed merely to present the evidence derived from cytological investigation and to discuss the phylogenetic groupings of those species of *Crepis* which have been investigated. These groupings, however, have been worked out by combining the data on chromosome number and morphology with the evidence from external morphology of the plants, at the same time giving consideration to geographic distribution and to the genetic evidence derived from experiments on interspecific hybridization.

The point of view held by the writers with regard to the fundamental relations between phylogeny and taxonomy is in general

agreement with that of Hall and Clements (1923). The concept of species defined by these authors and accepted by us as a satisfactory approximation to the truth is stated as follows:

> The evolutionary view of the species is that it is a definite phylogenetic stock, sprung from and related to similar stocks, and itself undergoing modification into a number of variads. As they have recently come from the same stock, these variads are more nearly related to each other than they are to those of any other species, and they represent a definite phylogenetic unit, the species, at the same time that they mark its further differentiation.

But the view of these authors, that gross morphological difference between plants, as contrasted with such cytological features as number and morphology of the chromosomes, is the only definite measure of progress in evolution, is too limited, as has already been pointed out by one of us (Babcock, 1924). The importance of the chromosomes, especially their appearance in somatic cells at mitotic metaphase, as an index of taxonomic relationship, has become increasingly evident as the number of species of *Crepis* examined has increased.

Acknowledgments

It is impossible at this time to mention the many institutions and individuals who have assisted by providing seeds or roots of the species herein discussed. These will appear in connection with sources to be acknowledged later. We are especially indebted, however, to Dr. M. Navashin for seeds of several species, which he brought from Russia, and for active interest and frequent help throughout the investigation. We also gratefully acknowledge the constant cooperation of Mr. C. W. Haney in connection with growing the plants, assisting in collection of root tips, and many other details.

CYTOLOGICAL MATERIALS AND METHODS

Somatic metaphases of root tips have been used exclusively for chromosome counts and morphological studies. In most cases the material was obtained from plants in the rosette stage after they had been transplanted to five- or six-inch pots. Occasionally the roots of very young seedlings were used but they were on the whole less satisfactory. Some of the counts on the American species were procured from tap roots dug from the wild and transplanted to pots in the greenhouse, where they produced new roots, giving material well suited for chromosome studies. In other American species the counts

were obtained from young seedlings. Introduction of most American species into garden culture has been found very difficult but is gradually being accomplished.

Roots were fixed in Taylor's (1925*a*) chrom-acetic-osmic-maltose solution, in weak and strong Flemming, and in chrom-acetic-formalin. Most of the investigations and all of the drawings have been made from material fixed in one of the two chrom-acetic-formalin solutions given below.

1. A. 65 cc. water
   10 cc. glacial acetic acid
   1 gr. chromic acid
   B. 40 cc. formalin (commercial)
   35 cc. water
   Mix one part A with one part B just before fixing.

2. A. 65 cc. water
   10 cc. glacial acetic acid
   1 gr. chromic acid
   B. 10 cc. formalin (commercial)
   65 cc. water
   Mix one part A with one part B just before fixing.

No constant difference in quality of fixation between material fixed in these two solutions has been established. The chromosomes fixed with these fixatives are usually slightly shorter and broader than those fixed in the osmic fixatives, so they may be somewhat contracted. Morphological details are quite clear in well fixed material, however, and in material so fixed the homogeneity of the cytoplasm, against which the chromosomes stand out very clearly, facilitates greatly the examination of the sections for suitable figures.

The material was imbedded in paraffin and sections were cut 6 to 12μ thick depending on the size and number of the chromosomes. Heidenhain's iron haematoxylin was used for staining.

A Bausch and Lomb (90×) apochromatic oil immersion-objective and Zeiss compensating oculars have been used in this study. All the drawings have been made with the help of a camera lucida at a magnification of approximately 3750 and reduced to 2500 in reproduction.

Where the chromosomes of a species were being investigated for the first time, counts from two or more plants were made whenever possible. The number of plants investigated is indicated in the table of chromosome numbers. In those instances where the chromosome number of a species newly investigated is based on one plant this plant is the only one which has been grown in our cultures. In the case of *Crepis incana,* the plant whose chromosomes were studied did not bloom; and as this was the only plant available and there were no herbarium specimens accompanying the seeds, the identification was based on achene and leaf characters alone.

Where the species had 12 or fewer chromosomes an attempt was made to find a metaphase plate, a drawing of which would depict the complex so that each individual chromosome might be recognized if it could be distinguished from the others under the microscope. Lack of sufficient material or particular difficulties have in some cases forced us to be satisfied with figures of plates which do not reach this ideal. In most cases, however, the chromosomes can be distinguished in the figures and the pairs recognized without difficulty.

Where the number exceeds 12, the problem of distinguishing the various chromosomes becomes more difficult and in most cases it has been impossible to distinguish all the chromosome pairs in one plate, although various types are readily picked out. In those species with more than twenty chromosomes the plates for drawing were chosen with the primary aim of depicting clearly the number, and, secondarily, of showing as many as possible of the chromosomes which could be distinguished by their particular morphology.

GENERAL MORPHOLOGICAL FEATURES

Marked differences in the frequency of occurrence of good metaphase plates were noted between species. The particular species in question, as well as the condition of the roots, affected the number of mitotic figures. Some species characteristically showed plates in which the chromosomes were well spaced in a single plane while in others the usual arrangement of chromosomes was such that a morphological study was impossible. The species with higher numbers and larger chromosomes presented greater difficulties in this respect.

Most species, in material well fixed in chrom-acetic-formalin and well stained, show black chromosomes, their outlines clear and distinct against the gray cytoplasm. When differentiated so as to clear the cytoplasm, some species show chromosome outlines which are less sharp, especially under high magnification. The extreme phase of this condition was found in certain species (*C. bulbosa* and *C. japonica*) which have been included under *Crepis* but which at one time or another have been assigned to other genera. The same is true of *Ixeris graminea*, which for a time was thought to belong in *Crepis*. Their chromosomes are small, and it may be that this is the reason why the outlines under differentiation become less clear so as to make it difficult to determine the shapes with exactness. The black and white figures used in this paper are not suitable for showing such differences.

Size difference continues to be one of the most useful features by which chromosomes may be distinguished. The relative lengths of the components of a particular chromosome complex are rather constant and although the lengths of the same chromosome may differ noticeably from cell to cell this variation is relatively small. Differences in the thickness of chromosomes of different species are obvious but no consistent difference between the widths of the various chromosomes of any one complex has been observed.

Satellites or "trabanten," chromatin balls attached to the chromosomes proper by thin threads, first described by S. Navashin (1912), are now generally recognized as of wide-spread occurrence. The list of plants and animals in which satellites have been observed, given by Kuhn (1928), will serve to illustrate in what diverse groups these peculiar structures occur. Most, if not all, species of *Crepis* contain at least one pair of chromosomes marked by the presence of satellites. They vary in size from a large ball (*C. setosa*, fig. 4*c*) to a tiny sphere (*C. palaestina*, fig. 18*d*). As in most other genera they are usually attached to the proximal ends (those which lie toward the center of the plate) of chromosomes which have short arms or heads (cf. below), but in some cases (*C. biennis*, fig. 12*a*) they may be attached to chromosomes with arms more nearly equal in length. In only one species (*C. pulchra* fig. 19) was there found a pair of chromosomes with distal satellites. In several species (*C. lyrata*, *C. mollis*, *C. hierosolymitana*, fig. 13) structures resembling large satellites at times, but at others appearing to be segments cut off by distal constrictions, have been seen. Such variations may be due to imperfect fixation as suggested by Taylor (1924). In this connection it should be noted that Geitler (1929) figured the chromosome complexes of *C. capillaris*, *C. dioscoridis*, *C. rubra*, and *C. blattarioides*, depicting morphological features similar to those shown in our figures. Considerable variation in the appearance of the satellited chromosome of *C. blattarioides* was described, including the form and size of the satellite and even its presence or absence. Some if not all of this variation can perhaps be attributed to poor fixation.

The behavior of the satellites during the mitotic anaphase of *C. capillaris* has been described and figured by Taylor (1926) and the writers' observations add nothing new to this knowledge. Whether or not the satellites are to be found on the nucleolus at prophase as stated by M. Navashin (1925) has not been particularly studied but prophases have been seen which could be interpreted as exhibiting this phenomenon.

The clearness with which the satellites are visible depends on their size, the quality of the fixation, and the degree of differentiation. The thread which attaches the satellite to the chromosome proper may be contracted under poor fixation until a small satellite appears as a little protuberance (*C. incarnata*, fig. 18*c*) or a large satellite as a segment. Excessive or even ordinary differentiation may render invisible a satellite thread or a small satellite. They are not always to be seen even in well fixed material but it is believed that in such cases they are hidden by the chromosomes proper and that they are constant morphological features of the living chromosome. The satellite may vary slightly in apparent size and shape from cell to cell within a species but on the whole it is as constant as any morphological feature. On occasion a satellite thread may be drawn out to an unusual length (*C. amplexifolia*, fig. 5*c*) or the spherical shape may be obliterated (*C. parviflora*, fig. 11*a*). These, however, are exceptional cases and may be due to poor fixation.

One certain case (*C. foetida* 2048, fig. 1*d*) and several possible cases of a constant difference in size between satellites on homologous chromosomes within a species have been found. M. Navashin (1926) reported such a case in *C. dioscoridis* and similar cases in other genera are known (cf. Kuhn, 1928). Detailed studies of more material would be necessary to decide the questionable cases.

Aside from size and the occurrence of satellites, a number of investigators have found that the most useful distinguishing feature of chromosomes is the occurrence of a fiber attachment constriction dividing the chromosome into two arms. The importance of the "two-armed" nature of the chromosomes has been reemphasized by Heitz (1928), who has found it in many widely separated families and indeed in different divisions of the plant kingdom, and he holds it to be a universal characteristic of chromosomes. S. Navashin (1916*b*) has stated that absolutely every chromosome possesses an "achromatic transverse fissure" which divides the chromosome into two arms (cited from M. Navashin, 1926). Taylor (1925, 1926), who has discussed fully the kinds of constrictions, has failed to find a case among any of the medium or large chromosome types studied which had a truly terminal fiber attachment and he is inclined to the opinion that an actual constriction zone or related structural differentiation is always present and can be demonstrated by suitable means. All investigators agree that one arm may be so short as to constitute a small head.

In *Crepis*, fiber attachment constrictions have been found on practically every chromosome which could be identified (except in *C. japonica* and *C. bulbosa*). Where the chromosome is bent so as to obscure the constriction, the relative lengths of the arms give a fair indication of its position, for the chromosome usually bends at the constricted region. The constrictions are particularly apt to be observed on chromosomes where they are to be found very near the ends, as on the satellited chromosomes of *C. alpina* var. *syriaca* Bornm.[1] (fig. 2*e*).

THE CHROMOSOMES OF SEVENTY SPECIES

Mann (1925) summarized the chromosome numbers of the twenty-seven species of *Crepis* reported by various investigators up to that time and Tischler (1927) has a complete bibliography of papers dealing with *Crepis* chromosomes which includes additional counts given by M. Navashin (1925), Babcock and Lesley (1926), and some unpublished chromosome counts by M. Navashin. The chromosome number of *C. reuteriana* has been given by Babcock and Hollingshead (1929). In no case have counts obtained by the writers differed from those reported by Mann, Navashin, or Babcock and Lesley.

With a few minor exceptions, no details of somatic chromosome morphology other than size differences were described in earlier works on the genus. De Smet (1913–14) figured satellites on *C. virens* (= *C. capillaris*) but did not describe them. Rosenberg (1918) recognized flexures in *C. tectorum* chromosomes as constant in position at somatic anaphase and later (1920) says, speaking of the chromosomes of *C. capillaris* (wrongly called *C. reuteriana*, cf. Babcock, 1924*b*), "ein sog. Trabantenbildung kommt vor die aber meiner ausicht nach von ganz anderer Natur ist als die 'Quersegmentierung.'" It is likely that the so-called "trabanten" which he saw were merely heads separated from the chromosomes proper by constrictions. De Litardière (1923) located the point of fiber attachment on one chromosome of *C. virens* (= *C. capillaris*) and noted that the chromosome was usually bent at that point. Mann (1925) saw the large satellite of *C. setosa* and stated later (Babcock and Lesley, 1926) that satellites were "not always present" in her material. Such results can, in most cases, be attributed to the use of unsuitable fixatives.

[1] This "variety" should be recognized as a distinct species, but the change in nomenclature will not be made at this time.

M. Navashin (1925, 1926) and Taylor (1925*b*, 1926) established the constant occurrence of satellites and fiber-attachment constrictions as features of use in distinguishing the various chromosomes in a number of species of the genus. Navashin (1925) figured ten species in which he had determined the morphological features of each chromosome. These species were *C. pulcherrima* (= *C. pulchra*), *C. grandiflora* (= *C. conyzaefolia*), *C. dioscoridis*, *C. tectorum*, *C. rubra*, *C. marschalli*, *C. virens* (= *C. capillaris*), *C. rhoeadifolia* (= *C. foetida*), *C. alpina*, and *C. parviflora*. To these he has added *C. aspera* in another paper (1927). Taylor (1925*b*) gave figures showing the morphological features of the various chromosomes of *C. setosa* and *C. capillaris*, and later (1926) he figured *C. capillaris* in somatic metaphases and anaphases. The investigations reported here have corroborated those of Navashin and Taylor in practically every detail, and drawings of the species they figured are included only for the sake of uniformity and completeness.

The present investigations add twenty-seven species to the list of those whose chromosome numbers are known (including four species of other genera closely related to *Crepis*). Table 1 gives the somatic

TABLE 1

THE SOMATIC CHROMOSOME NUMBERS OF SIXTY-SEVEN SPECIES OF CREPIS

(Three other species are listed, with numbers in italics, which are not accepted in *Crepis* by the authors.)

OLD WORLD SPECIES

Species	Somatic chromosome number	Number of plants examined	Accession
C. aculeata (DC.) Boiss.	8	2	1602
C. alpina L.	10	1	1499
**C. alpina* var. *syriaca* Bornm.	10, 11, 12, 13	20	1923
C. amplexifolia (Godr.) Willk.	8	5	1019
C. aspera L.	8	2	1135, 1973
**C. asturica* Lacaita	10	3	2088
C. aurea (L.) Cass.	10	2	2170
C. biennis L.	39, 41	5	1874, and others
C. blattarioides (L.) Vill.	8	1	2033
C. bulbosa (L.) Tausch	*18*	*3*	*1303*
**C. bungei* Ledeb.	8	16†	1827
	16	3	2174
**C. burejensis* F. Schmidt	8	5	2747
C. bureniana Boiss.	8	8	1655

* Chromosome number reported for the first time.

† One plant was triploid with 12 chromosomes.

TABLE 1—(*Continued*)

Species	Somatic chromosome number	Number of plants examined	Accession
C. bursifolia L.	8	3**	1220
C. capillaris (L.) Wallr.	6	20	X, 982 and others
C. chondrilloides Jacq.	8	2	2180, 1907
**C. chrysantha* Froel.	8	3	2179
C. ciliata C. Koch	40, 42?	2	2181
C. conyzaefolia (Gouan) D. T.	8	2	2183
C. dioscoridis L.	8	3	1742, 972, 1455
C. foetida L.	10	3	1751, 2188
		1	2048
		3	2307
**C. gymnopus* Koidz.	8	2	2746
**C. hackeli* Lange	16	3	1873
**C. hicrosolymitana* Boiss.	12	3	2619
C. hookeriana Ball	8	1	1458
**C. incana* Sibth. et Sm.	16	1	1667
C. incarnata Tausch	8	1	1304
C. japonica (L.) Benth.	*16*	*2*	*1045, 2132*
C. lacera Tenore	8	4	1914
**C. leontodontoides* All.	10	1	1807
**C. lybica* Pamp.	8	1	1698
C. lyrata Froel.	12	4	1644
C. marschalli C. A. Mey.	8	3	1532
C. mollis (Jacq.) Asch.	12	2	2201
C. montana Urv.	12	2	1175
C. multicaulis Ledeb.	10	2	1480
C. myriocephala Coss. et DR.	8	1	1557
**C. nana* Richards.	14	2	2698
C. neglecta L.	8	1	1753
C. nicaecnsis Balb.	8	6	2700
C. palaestina (Boiss.) Bornm.	8	1	1552
C. paludosa (L.) Moench	12	1	1825
C. pannonica (Jacq.) C. Koch	8	1	1695
C. parviflora Desf.	8	2	1630
**C. pontana* (L.) D. T.	10	2	2204
C. praemorsa (L.) Tausch	8	3	2133
C. pulchra (L.)	8	4	1213, 1483
		1	1894
C. reuteriana Boiss.	8	4	2134, 2218
C. rubra L.	10	2	1506
		1	1176
C. senccioides Delile	8	5	1044
C. setosa Hall. f.	8	1	1036
		1	1510
C. sibirica L.	10	2	1862
C. taraxacifolia Thuill.	8	5	1806, 1064, 1704
		1	1895

* Chromosome number reported for the first time.

** One plant was a trisomic with 9 chromosomes.

TABLE 1—(*Continued*)

Species	Somatic chromosome number	Number of plants examined	Accession
C. tectorum L.	8	9	1498
		1	1702
**C. tenuifolia* Willd.	15	8	1826
C. tingitana Salz.	10	1	1681
C. vesicaria L.	8	4	1576
**Rodigia commutata* Spr.	10	2	1666, 2219
**Ixeris graminea* Nakai	*16*	*2*	*2568*
**Pterotheca sancta* (L.) K. Koch	10	1	2582 or 2583
AMERICAN SPECIES			
	44?	1	1778 (typical)
	33	6	1922 (typical)
	33	1	2096 (typical)
**C. acuminata* Nutt.	55?	1 or more‡	1830 (form)
	33	1 or more	1848 (form)
	33	4	1919 (form ?)
	33	4	1934 (hybrid form)
**C. andersoni* Gray	22	3	2086 (typical)
	22	2	2136 (form)
**C. elegans* Hook.	14	5	2654
**C. barbigera* Leib.	88?	1 or more	1840 (typical)
	88?	1 or more	1842 (typical)
	44	1 or more	1838 (hybrid form)
	88?	6	1959 (hybrid form)
**C. glauca* (Nutt.) T. and G.	22	1 or more	2079 (typical)
**C. gracilis* (Eat.) Rydb.	22	2	2572 (typical)
	55?	6	1695 (form)
**C. monticola* Coville	55?	1 or more	2771 (typical)
C. nana (see Old World Species)			
	22	2	2772 (typical)
**C. occidentalis* Nutt.	22?	1	2220 (form)
	44	5	1921 (form)
	22	1	1829 (form)
	22	1	2075 (form)
	22	1	2078 (form)
	22	1	2066 (form)
	22	2	2065 (form)
**C. runcinata* (James) T. and G.	22	1	2068 (form)
	22	1	2069 (form)
	22	1 or more	2076 (form)
	22	2	2077 (form)
	22	1	2083 (form)
	22	1	2071 (form)
**C. scopulorum* Cov.	44?	2	2773 (form)

* Chromosome number reported for the first time.

‡ Indicates that the roots were fixed under the accession number only and no record was kept of the number of plants fixed together.

chromosome numbers of the species, the chromosomes of which are described below, the numbers of individual plants, and the accession numbers of the various plants examined. An accession number is given to each lot of seeds or roots when it is received and the progeny of any accession is likewise designated by that number. An asterisk denotes that the chromosome number is reported for the first time. Three of the species designated by asterisks (*C. lybica*, *C. runcinata*, and *C. glauca*) were first counted by Dr. Margaret Mann Lesley and one (*C. leontodontoides*) was first examined by Miss Priscilla Avery (unpublished observations).

With the discovery of the somatic number 14 in *C. nana*, the known series of somatic chromosome numbers in the Old World species of *Crepis* becomes 6, 8, 10, 12, 14, 15, 16, and 40±. That of the American species is 14, 22, 33, 44, 55?, and 88?.

In the following descriptions the species are taken in groups corresponding to the phylogenetic groups to be considered later. There are four major groups or subgenera—**Paleya**, **Barkhausia**, **Catonia**, and **Eucrepis**. The arrangement of species within each of these divisions is shown in the chart on page 30.

Paleya

Crepis asturica ($2n = 10$; fig. 1*a*), the one representative of the subgenus **Paleya** which has been examined cytologically, has a complex which illustrates several of the chromosome types common in the genus. The two longer pairs, nearly equal in length, can be distinguished from one another by a small difference in the relative lengths of the arms which are separated by the fiber attachment constrictions. The satellited pair, shorter, has the fiber attachment constrictions closely subterminal, forming small heads to which the small satellites are attached. The two remaining pairs, nearly equal in length to the satellited pair, have fiber attachment constrictions median or nearly median and they commonly appear as small V's.

Barkhausia

The chromosomes of *C. alpina*, *C. alpina* var. *syriaca*, *C. rubra*, *C. foetida*, and *Rodigia commutata*, all with a somatic number of ten, resemble those of *C. asturica* but with the exception of *C. rubra* they are generally smaller. Those of *C. foetida* (fig. 1*b*, *c*, *d*) resemble those of *C. asturica* most closely and are almost as large.

C. foetida 2188 (= *C. rhoeadifolia*, Navashin, 1925) does not differ noticeably from typical *C. foetida* in chromosome morphology, nor does *C. foetida* 2307 (= *C. glandulosa* Guss.), but *C. foetida* 2048 (= *C. interrupta* S. et S.) is distinguished by larger satellites and the plant examined showed a marked difference in the size of the two satellites (fig. 1*d*). That a careful study involving investigation and measurement of many chromosomes might establish further differ-

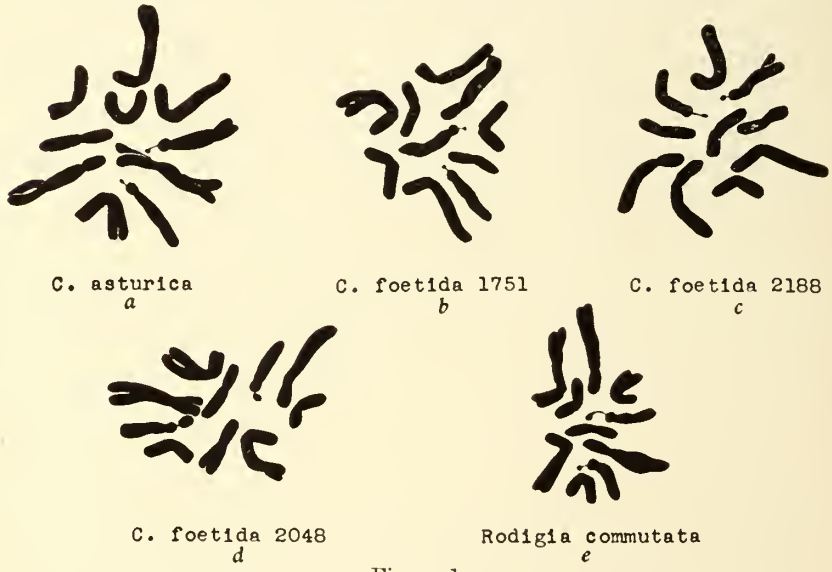


Figure 1.

ences between these *foetida* strains cannot be denied. *Rodigia commutata* (fig. 1*c*) has a chromosome complex very similar to that of *C. foetida*.

In *C. alpina* (fig. 2*a*) one of the two short pairs of chromosomes has small heads. Plants of *C. alpina* var. *syriaca* (fig. 2*b*, *c*, *d*, *e*) which were examined varied in chromosome number from 10 to 13. Table 2 gives the number of plants counted and their origins. With one exception only the first root of a seedling was examined and in many cases it was not possible to determine the shapes of all the chromosomes. However, it was established that at least some of the plants with 10 chromosomes had a chromosome garniture which differed noticeably from that of *alpina* in the shape of one of the small pairs. As far as could be determined the variation in number involved a small chromosome with a head to which was attached a rather large satellite, the 10-, 11-, 12- and 13-chromosome plants

TABLE 2

THE SOMATIC CHROMOSOME NUMBERS FOUND IN C. ALPINA VAR. SYRIACA

Origin of seed	Culture number	Number of plants with chromosome numbers of			
		10	11	12	13
Univ. Calif. Herbarium sheets 313831 and 313832*	27.1923			1	
Univ. Calif. Herbarium sheet 313832	28.1923A	6	1		
27.1923–2 open pollinated	28.1923B	1	3	5	3

*Several plants collected in Galilee, Palestine, environs of the Menahamiah Company, April 20, 1924, by M. Chijik.

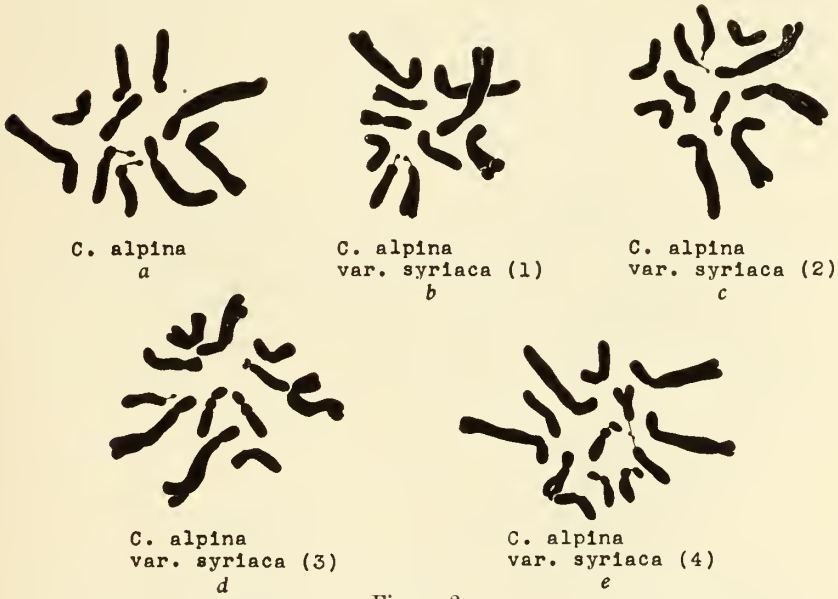


Figure 2.

having none, 1, 2, or 3 of these chromosomes respectively. This situation recalls that of the supernumerary chromosomes in maize (Randolph 1928*a* and *b*) and merits further study.

The chromosomes of *C. rubra* (fig. 3*a*, *b*) are larger than those of *C. asturica* and they differ in other respects, the most noticeable of which is the occurrence of a pair of short chromosomes with large, often constricted, satellites. No other satellites were seen in *C. rubra* 1506 but in *rubra* 1176 one chromosome pair bore very small satellites. M. Navashin (1925) shows the small satellites in his figure of *rubra* but in strains examined later he failed to find it (unpublished observations).

Figure 3.

Crepis aspera, *C. bursifolia*, *C. setosa*, and *C. senecioides* (fig. 4), with 8 chromosomes each, are quite different in details of their chromosome morphology. *C. setosa* is characterized by the presence of a pair of large satellites and *C. senecioides* is outstanding among the 8-chromosome species by the small size of its chromosomes.

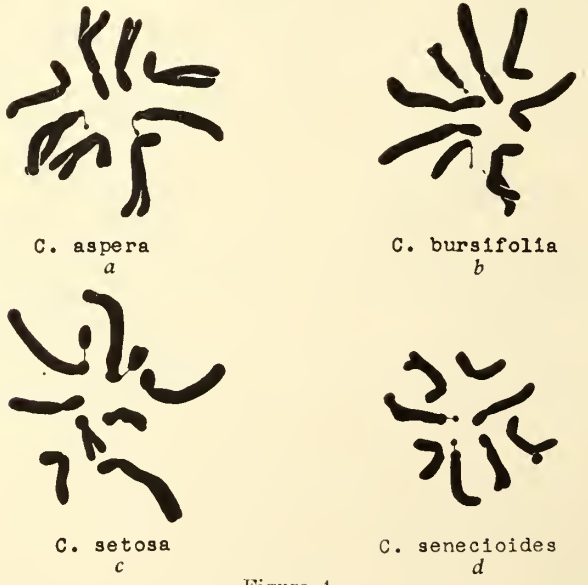


Figure 4.

Crepis bureniana, *C. aculeata*, and *C. amplexifolia* (fig. 5) with 8 chromosomes, are quite distinct in chromosome morphology. *C. bureniana* and *C. aculeata* have chromosomes of the same size order; those of *C. amplexifolia* are smaller. The exact position of the fiber attachment constriction on one chromosome of *bureniana* has not been determined, owing probably to inferior fixation, but it is very near the end.

Figure 5.

The chromosome garnitures of *C. myriocephala* ($2n = 8$) and *C. lybica* ($2n = 8$, fig. 6*a*, *b*) appear to be indistinguishable from each other and differ only in their slightly larger size from those of *C. vesicaria*, *C. taraxacifolia*, and *C. marschalli* (fig. 6*c*, *d*, *f*) which are extremely similar to one another.

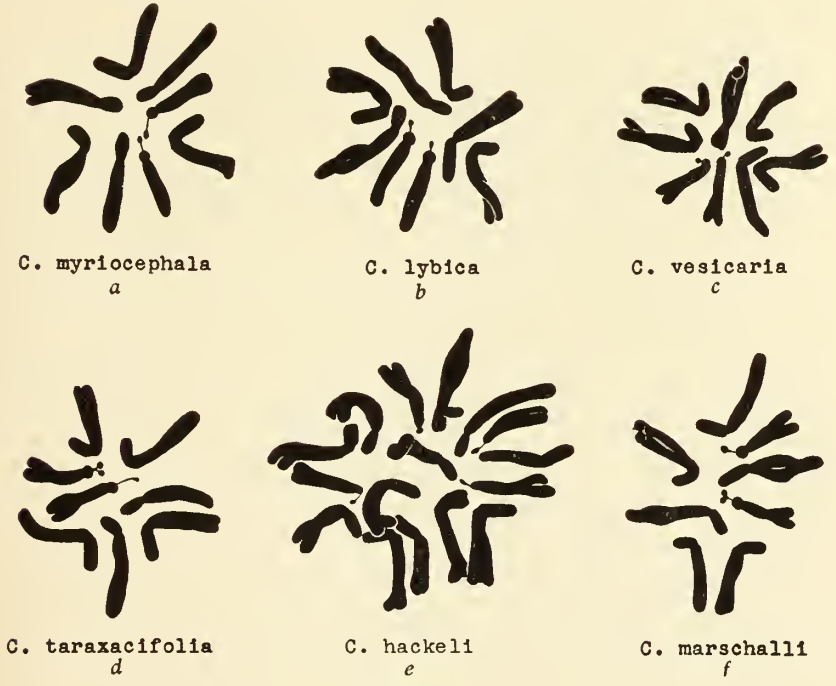
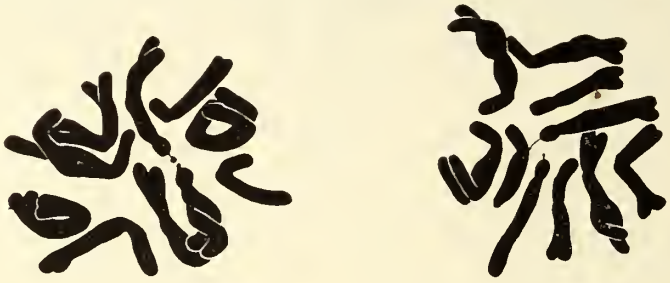


Figure 6.

Crepis hackeli ($2n = 16$, fig. 6*e*) is probably a tetraploid species. Good plates showed 4 similar satellited chromosomes resembling closely those seen in *vesicaria*, etc., and 4 chromosomes resembling the

largest of those in the same group of species. The increased number did not permit an exact comparison of the remaining chromosomes which are rather similar in morphology. They do, however, resemble in shape and size the intermediate chromosomes of the *vesicaria* group.



C. sibirica
a

C. pontana
b

Figure 7.

Catonia

Crepis sibirica and *C. pontana* ($2n = 10$) have chromosome complexes which differ in details but are similar in size and much larger than those of any other 10-chromosome species examined (fig. 7). In the plate of *C. sibirica* figured, one of the satellite threads has contracted so that the satellite appears as a small protuberance on the proximal end of the chromosome. This is not a constant condition.

Crepis blattarioides ($2n = 8$, fig. 8*a*) has, on the whole, chromosomes slightly smaller than those of other species of this phylogenetic line. One pair bears rather large satellites. *C. burejensis*, *C. chrysantha*, and *C. conyzaefolia* (fig. 8*b*, *c*, *d*) have similar garnitures of 8 large chromosomes, the first differing noticeably from the other two in the shape and size of the satellited chromosome. In the plate from which the figure of *C. chrysantha* was drawn, one of the satellites, two of which were found in other plates, was apparently hidden by another chromosome.

Crepis paludosa ($2n = 12$) is easily distinguished from the other species of this subgenus which have been examined cytologically by the number and shape of its chromosomes (fig. 8*e*).

In *C. aurea* ($2n = 10$, fig. 9*a*) the chromosome complex resembles that of *C. asturica*, differing markedly from it in only one chromosome pair. The chromosomes of *C. bungei* 1827 ($2n = 8$, fig. 9*c*) are larger than those of *C. hookeriana* ($2n = 8$, fig. 9*b*). *C. bungei* 2174 ($2n = 16$, fig. 9*d*) has chromosome types resembling those of *C.*

bungei 1827 but they appear to be slightly smaller. Although several of the chromosome types in the 16-chromosome race may be represented more than twice, only two satellited chromosomes were seen and M. Navashin, from whom the material was obtained, has not seen

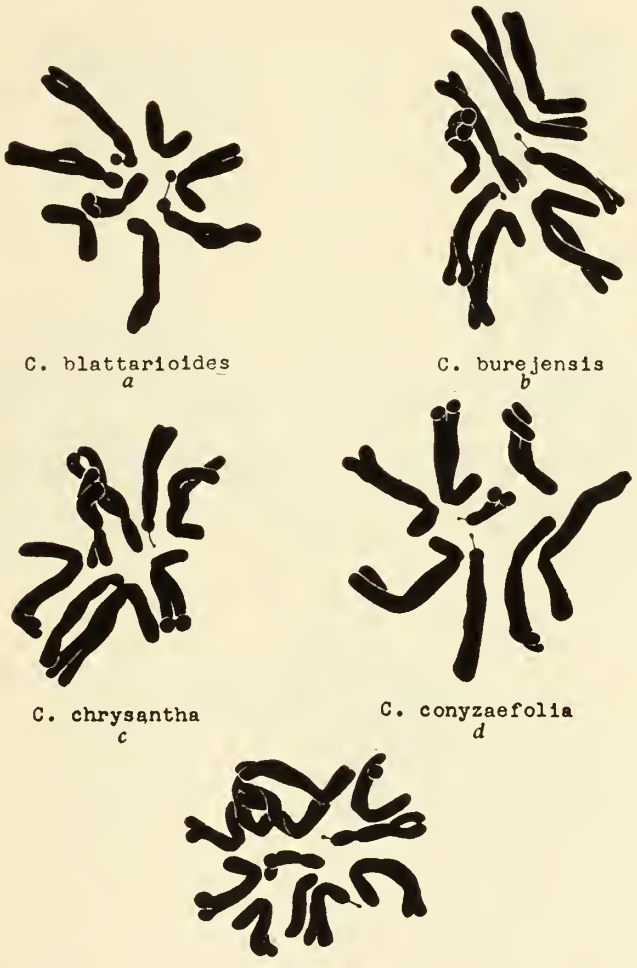


Figure 8.

more in similar material (unpublished observations). Plants of these two accessions are now in flower. Although 1827, with 8 chromosomes, is more nearly typical of the species in shape of leaves and habit of branching, yet the flower-heads and finer details of the

inflorescence are very similar in the two. Apparently 2174, with 16 chromosomes, is a form of this species resulting from some sort of chromosomal variation, the precise nature of which can be determined only by further study.

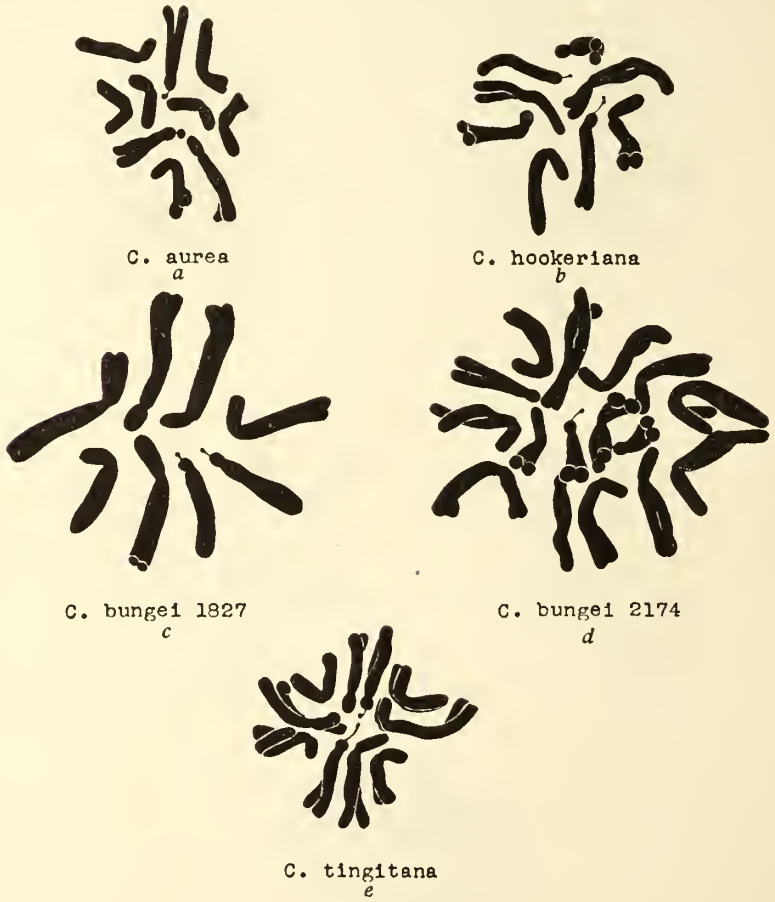


Figure 9.

C. tingitana ($2n = 10$, fig. 9*c*) has chromosomes resembling those of *C. asturica* but differing markedly from them in one chromosome pair.

Eucrepis

The chromosomes of *C. leontodontoides* ($2n = 10$, fig. 10*a*) and *C. multicaulis* ($2n = 10$, fig. 10*b*) are noticeably different in size, those of *C. multicaulis* approaching those of *C. asturica*, those of *C.*

leontodontoides being much smaller. Both complexes differ in other details from that of *C. asturica* and from each other.

C. tectorum ($2n = 8$), *C. neglecta* ($2n = 8$), *C. parviflora* ($2n = 8$), *C. capillaris* ($2n = 6$), and *C. nicaeensis* ($2n = 8$) do not particularly

Figure 10.

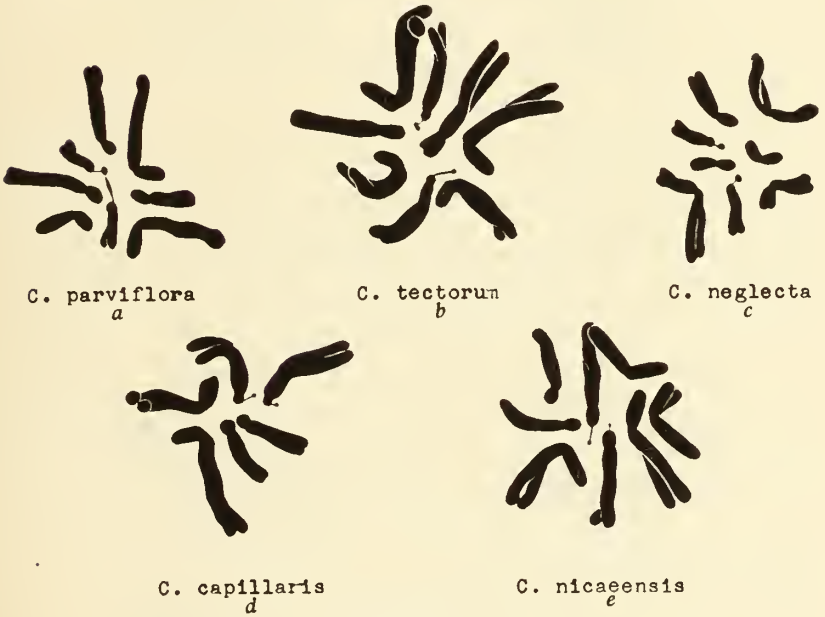


Figure 11.

resemble each other in chromosome morphology (fig. 11). Those of *neglecta* are the smallest, those of *tectorum* the largest of this series.

In *C. biennis* the chromosome number has been variously reported as $n = 16$ (Marchal, 1920), $n = 20$ (Rosenberg, 1918), $n = 21$, $2n = 42$ (Rosenberg, 1920), and $2n = 40$ (Mann, 1925). Investigations of several plants (table 1) have shown that there is an actual variation in number from plant to plant and this is confirmed by

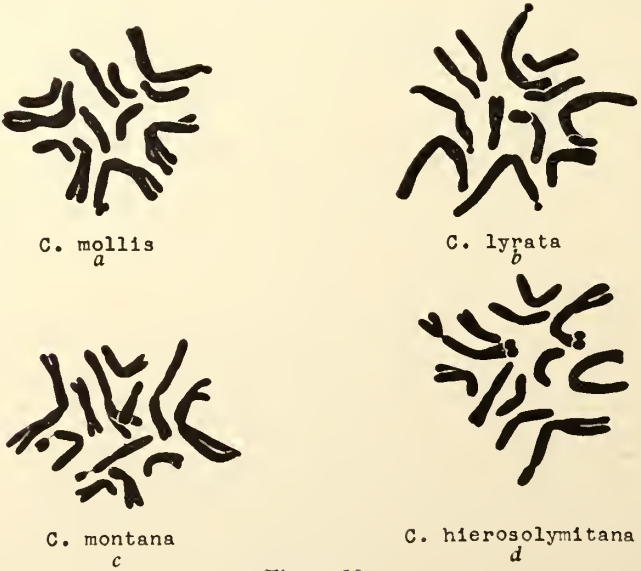
unpublished observations of M. Navashin (cf. Collins, Hollingshead, and Avery, 1929). Counts of 39 and 41 have been obtained and the plant from which the plate in figure 12*a* was drawn had 39 chromosomes. Satellites have been seen on chromosomes of at least two different types but those on only one type were visible in this figure.

C. biennis
a

C. ciliata
b

Figure 12.

A similar situation with respect to variation in number was found in *C. ciliata* (fig. 12*b*) the two plants examined having 40 and 42? chromosomes respectively. The latter count is not well established but there were more than 40 chromosomes. Again satellites were seen but the large number of chromosomes precluded a



C. mollis
a

C. lyrata
b

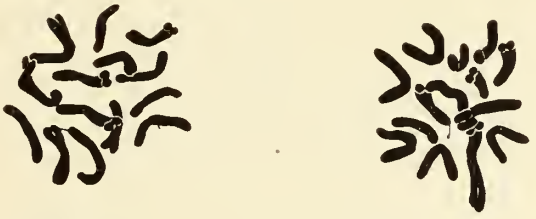
C. montana
c

C. hierosolymitana
d

Figure 13.

decision as to their exact number. The chromosomes of *C. biennis* and *C. ciliata* are of the same size order.

The group of four species with $2n = 12$ (fig. 13), *C. mollis*, *C. lyrata*, *C. montana*, *C. hierosolymitana*, gave material on which it was somewhat difficult to make out exact details of chromosome morphology. The chromosome outlines were not quite so clear as in most species and the increased number added to the difficulty. True satellites were found in *montana* and distal constricted ends which often resembled satellites were found on V-shaped chromosomes of *lyrata*, *mollis*, and *hierosolymitana*. Whether there are other small true satellites has not been definitely decided.



C. nana
a

C. elegans
b

Figure 14.

The material of *C. nana* and *C. elegans* ($2n = 14$, fig. 14*a*, *b*) was limited to a few root tips from germinated seeds and the figures available were anything but satisfactory for a study of chromosome morphology though the number was quite clear. The complexes are similar, containing long and medium V's and probably a satellited pair of chromosomes with submedian constrictions. In each of the figures reproduced only one satellite appears, but in *C. nana* other plates were seen containing two satellites.

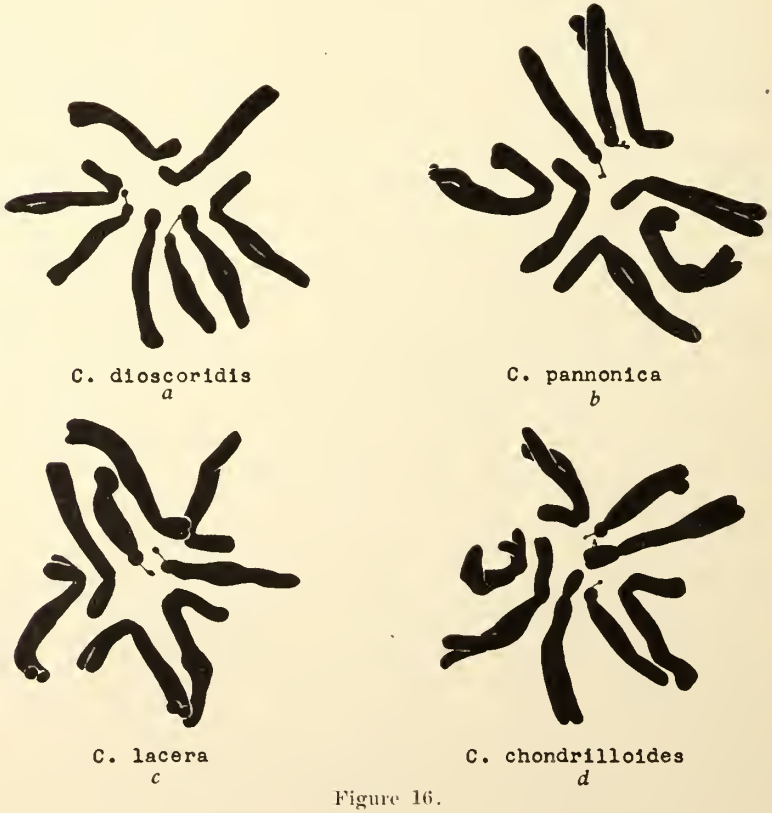
Extensive study of material from six plants of *C. tenuifolia*, grown from seed collected from the wild, revealed always a somatic number of fifteen chromosomes. Two of these plants have flowered with the help of artificial light and one produced a number of achenes. Two plants which grew from these achenes were examined and each had 15 chromosomes. Reduction divisions of the plants which flowered were very irregular showing sometimes 15 univalent chromosomes and sometimes both bivalents and univalents. An examination of the somatic chromosomes (fig. 15*a*) shows no good evidence of hybrid origin since many of the chromosomes have seemingly morphological mates. In the plate drawn, the upturned chromosome lying beneath

C. tenuifolia
a

Pterotheca sancta
b

Figure 15.

another in the central region is probably similar to the short one in the middle lower portion of the figure. This was the only plate observed in which there appeared to be 4 satellited chromosomes although 3 were seen very commonly. Whatever the origin of this species the evidence points to some form of parthenogenesis or apogamy as the usual means of reproduction. This would reconcile the irregularity in reduction divisions and low proportion of good pollen



C. dioscoridis
a

C. pannonica
b

C. lacera
c

C. chondrilloides
d

Figure 16.

with the apparently constant odd number of chromosomes and the fairly high proportion of achenes obtained.

Pterotheca sancta ($2n = 10$, fig. 15*b*) has chromosomes of the *C. foetida* type. We are indebted to Dr. M. Navashin for kindly giving us the opportunity of reproducing the figure from his slide. In this, the only plant examined, apparently one of the short chromosome pairs was heteromorphic, the spindle-fiber attachment of one chromosome being median, and of its mate being submedian.

C. dioscoridis, *C. pannonica*, *C. lacera*, and *C. chondrilloides* (fig. 16) have eight chromosomes in garnitures which resemble each other and those of *C. burejensis*, *C. chrysantha*, and *C. conyzaefolia* of the

C. incana

Figure 17.

subgenus **Catonia** (above). The chromosomes of *dioscoridis* seem to be slightly smaller and those of *pannonica* slightly larger than those of the other species in this group. *C. incana* ($2n = 16$, fig. 17) is probably a tetraploid species since it has 4 similar chromosomes in each set. The chromosomes resemble those of the group just described.

The complexes of *C. reuteriana*, *C. praemorsa*, *C. incarnata* and *C. palaestina* (fig. 18), and of *C. pulchra* and *C. gymnopus* (fig. 19), with 8 large chromosomes, are similar, those of *C. incarnata* and *C. praemorsa* being probably indistinguishable. Each of these species is characterized by the presence of one pair of long V-shaped chromosomes. Each has a pair of very small satellites. On the shortest chromosome pair of *C. pulchra* in well fixed, darkly stained material there could be found very small distal satellites. These have not been seen in other species. This pair of chromosomes differed in shape

C. reuteriana
a

C. praemorsa
b

C. incarnata
c

C. palaestina
d

Figure 18.

C. pulchra (1)
a

C. pulchra (2)
b

C. pulchra (3)
c

C. gymnopus
d

Figure 19.

in the strains of *pulchra* examined. In one strain (1213, fig. 19*c*) a plant occurred in which the attachment constriction of one of the members of the pair was nearly median, in the other member it was distinctly nearer the proximal end. In another plant of the same strain (fig. 19*b*) in both members of the pair the constriction was median. In plants of two other strains (1483 and 1894) each member of the pair had the constriction nearer one end of the chromosome (fig. 19*a*).

Figure 20.

The chromosomes of the American species (except *C. nana* and *C. elegans*) (figs. 20 to 22) are intermediate in size and the various species show similar types of chromosomes. Satellites have been seen in nearly every species but only in some of the 22-chromosome forms was it possible to determine their number, 4 satellited chromosomes having been established in several cases.

The *C. occidentalis*, *monticola*, *scopulorum* and the *C. gracilis*, *acuminata*, *barbigera* groups (figs. 20 and 21) show polyploid series with a base number of 11 (table 1). In some cases, indicated by (?) after the chromosome number, the large number of chromosomes or paucity of material has prevented an exact determination but the number

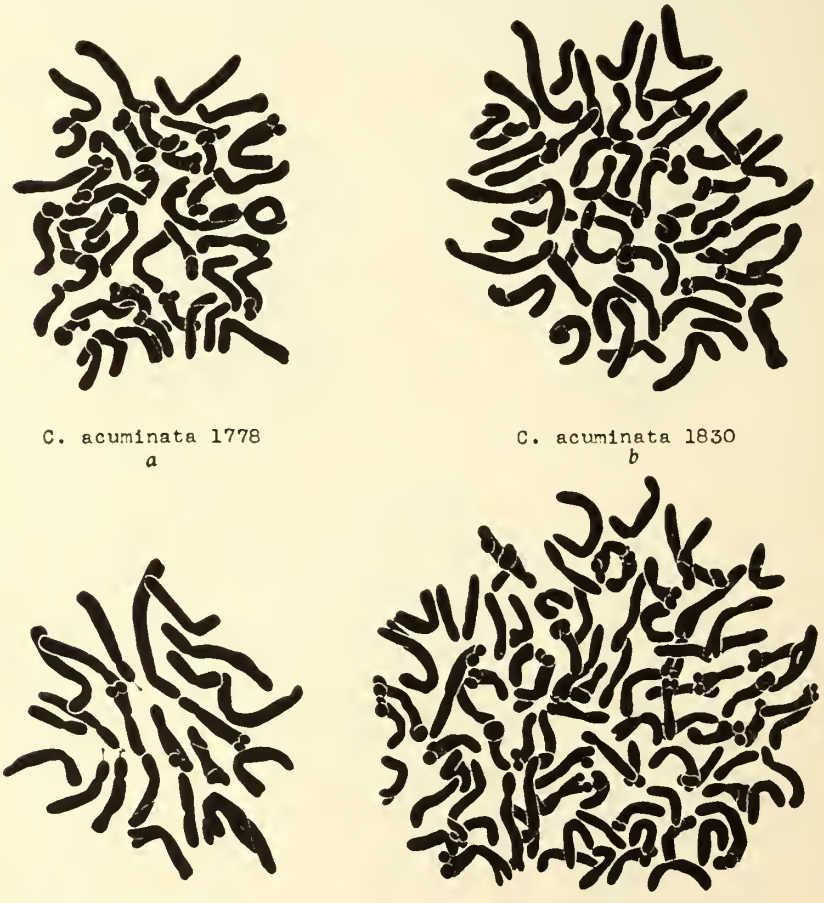


Figure 21.

given was the most likely one. In *C. occidentalis*, *C. gracilis*, and *C. acuminata*, variation in number between different forms has been found. The occurrence of the odd numbers 33 and 55 point to natural crossing and there is abundant morphological evidence that natural crossing, even between species, is no uncommon occurrence. The occurrence of the numbers 33 and 44 in typical *C. acuminata* suggests

the possibility that the somatic number 22 exists in this species, too, as it does in *occidentalis* and *gracilis*.

The *C. andersoni, glauca, runcinata* group (fig. 22) of which several plants representing different accessions (table 1) have been

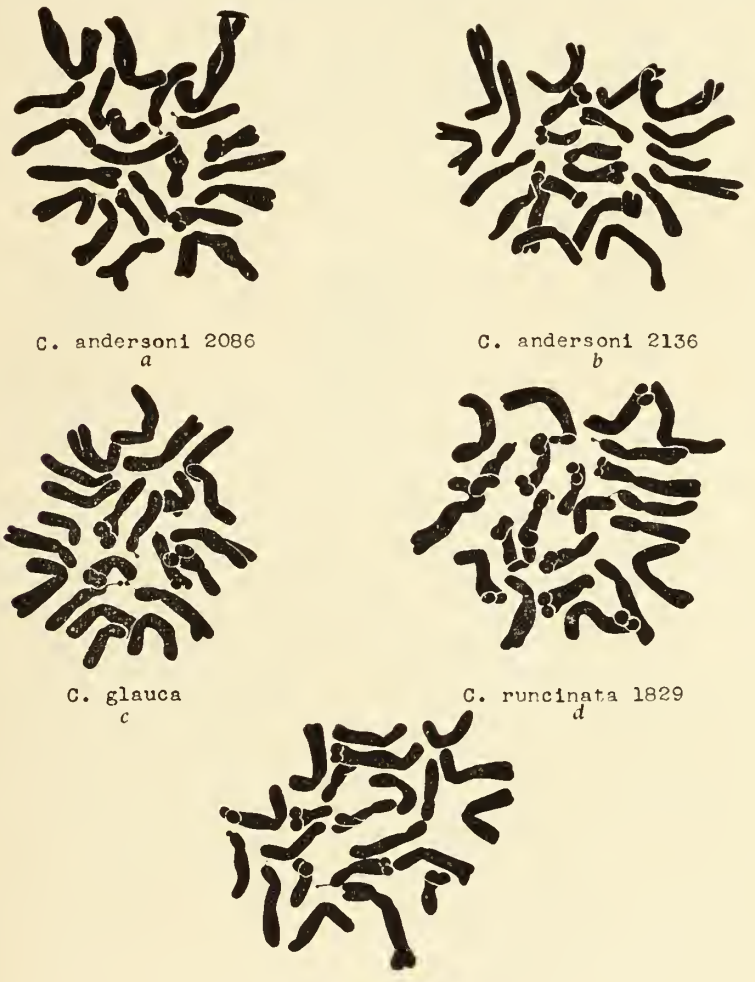


Figure 22.

examined, has given uniformly complexes of 22 chromosomes containing similar types. Whether it would be possible by a prolonged study to reveal differences in chromosome morphology between these species cannot be said.

Ixeris graminea ($2n = 16$), *C. bulbosa* ($2n = 18$), and *C. japonica* ($2n = 16$), while apparently representing the three large subgenera in certain morphological features, have chromosomes whose morphology has much in common and which differ from the other species described so noticeably that they are grouped together for descriptive purposes (fig. 23). The general features in which they differ, size and sharpness of outline, have been noted earlier. In each species the shapes of most of the chromosomes suggest median or submedian fiber attachments. At least one pair of chromosomes in each bears satellites or structures resembling them.

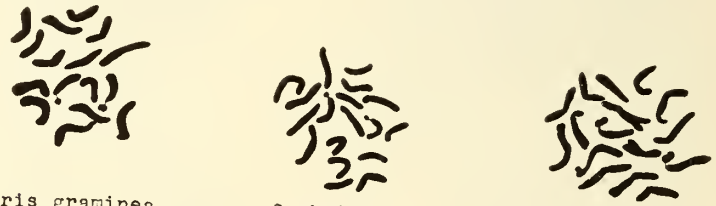


Figure 23.

THE PHYLOGENY OF SIXTY-SEVEN SPECIES OF CREPIS

The phylogenetic relations between the four subgenera, as at present understood, are fairly well represented by the four major divisions of the chart, figure 24, in which **Paleya** occupies the center, **Barkhausia** the upper right portion, **Catonia** the upper left, and **Eucrepis** the lower half. The relations between the species in each subgenus are indicated by the arrangement in groups and by lines leading to or toward the region of origin in the center. The chromosome number of each species is also given but in order to compare chromosome morphology it will be necessary to consult the figures presented in foregoing pages.

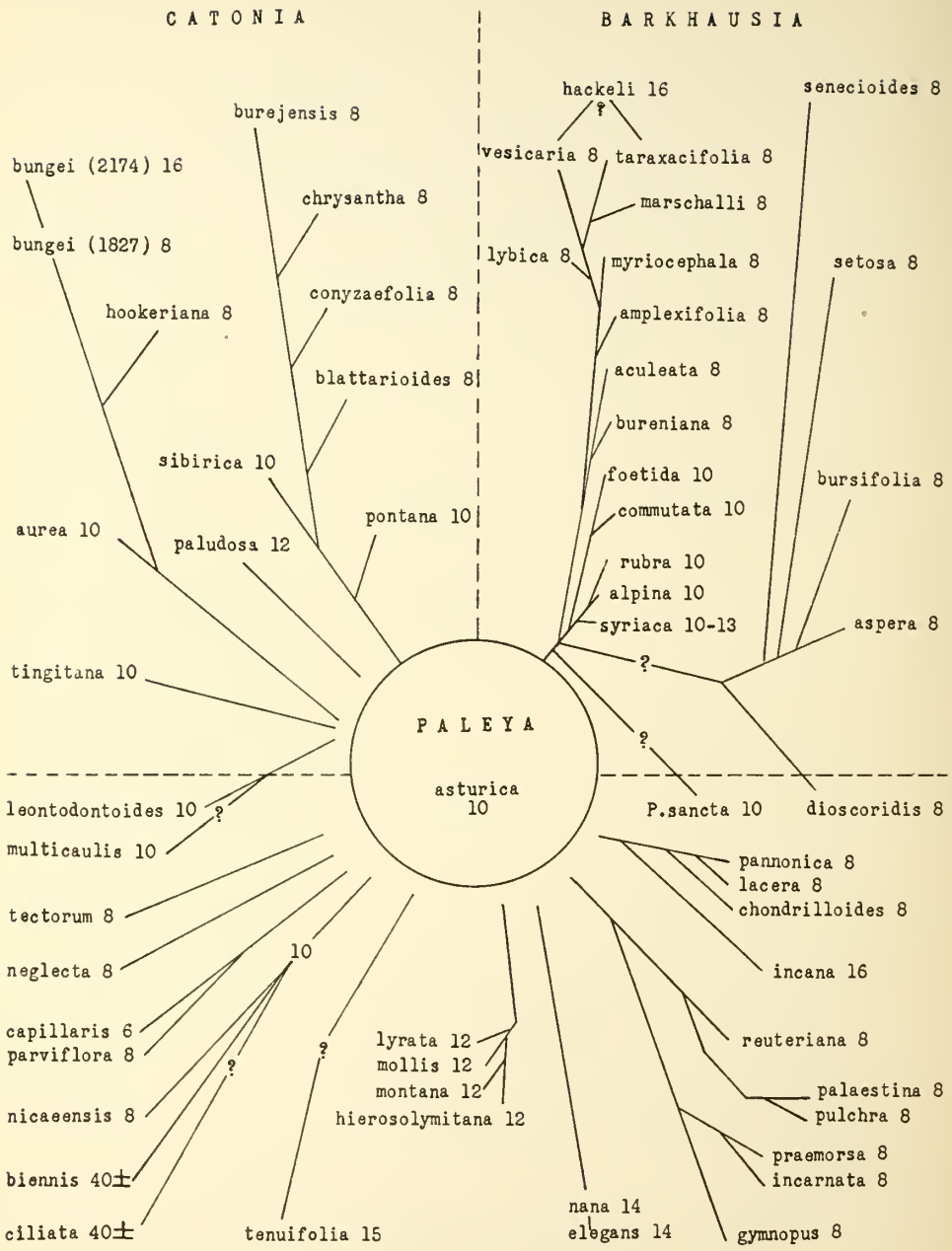
Paleya

Paleya is certainly the most primitive of the four subgenera. It contains only four or five species which are all perennials of restricted distribution but which occupy very widely separated areas (southwestern Europe, Abyssinia, and western Himalaya). In these species, unlike other *Crepis*, the involucre is not clearly differentiated into outer and inner series of bracts, at least as regards length, although

in one species the outer bracts differ in color from the inner ones. The leaves are large and nearly entire and the heads are few and large. The achenes are large, elongate, and in three or four of these species they are more like **Barkhausia** achenes while in the other they are more like those of **Catonia.** *C. asturica* is one of those with **Barkhausia**-like achenes and the marked similarity between its chromosomes and those of *foetida* and its close relatives has been noted. It seems reasonable to assume that **Paleya** was formerly a widespread group containing more numerous species than at present and that among these species there existed primitive forms of all three of the other subgenera. As most of these primitive forms are now extinct, evidence is lacking for direct connection between **Paleya** and some **Catonia** species and between **Paleya** and all **Eucrepis** species.

Barkhausia

Of the other three subgenera, **Barkhausia** exhibits its relationship to **Paleya** most obviously both in external morphology and in chromosomes, but it must be remembered that as yet the chromosomes of only one species of **Paleya** have been seen. **Barkhausia** contains about one-fourth of the species under discussion; these occur in portions of Europe, Asia, and Africa bordering on the Mediterranean. A few of these species are of wide distribution within the area defined, but most of them are of rather restricted range. The species of **Barkhausia** are all characterized by having definitely beaked achenes in which the beak is usually equal to or longer than the body of the fruit. This specialization for seed dispersal indicates considerable advancement beyond **Catonia** and **Eucrepis,** but, as was noted above, the line of development is well advanced in most of the present species of **Paleya.** There is also present in **Barkhausia** a strong tendency to have the marginal achenes different from the inner ones either in shape or in color and texture of the pericarp or in both respects, and in some species, like *alpina*, *aspera*, and *aculeata*, these differences in outer and inner achenes are very striking. Although a few species of **Eucrepis** have strikingly modified marginal achenes and it is not uncommon in both **Eucrepis** and **Catonia** to find the marginal achenes slightly different in shape from the inner ones, yet in neither of these subgenera is found as great specialization of the marginal achenes as occurs in **Barkhausia.** Nearly all species of **Barkhausia** are annuals which may also be taken as evidence of more recent development than in **Catonia** and most **Eucrepis.** There is much variation among these



occidentalis 22,44	gracilis 22,55?	glauca 22
monticola 55?	acuminata 33,44,55?	andersoni 22
scopulorum 44?	barbigera 88?	runcinata 22

Figure 24. EUCREPIS

species and within some of them, in leaf characters, number and size of heads, and size of achenes.

Anisoderis, a subgroup of **Barkhausia,** contains the species most resembling **Paleya.** This subgroup originally contained *C. alpina, rubra,* and *foetida,* and to these may be added two species now known as *C. alpina* var. *syriaca* and *Rodigia commutata.* The close resemblance between the chromosomes of these species and those of *C. asturica* has been noted. All the other species of **Barkhausia** have 8 (or 16) chromosomes. Their arrangement in the chart, figure 24, is based primarily on external morphology, particularly on achene characters, and the achenes of some of them have been illustrated in an earlier paper (Babcock and Lesley, 1926). Although *aspera* and *aculeata* are rather closely related, their very different achenes show their relationship to different species. Thus *aspera* most nearly resembles *dioscoridis* (of **Eucrepis**) in its marginal achenes, while its inner ones are more like those of *bursifolia, setosa,* and *senecioides,* but these five species are all widely separated from one another in other characters. It may be that the *aspera* line and the *aculeata* line arose from a common stock of distinct origin from the *alpina* line, the supposed progenitor being some (extinct?) species of **Paleya** having 8 chromosomes. For present purposes, however, it is more convenient to indicate these two lines as arising from the *alpina* line.

The four species, *bureniana, aculeata, amplexifolia,* and *myriocephala* differ from the remaining five species, grouped near the top, in having the marginal achenes distinctly different from the inner ones. *C. bureniana* most nearly resembles *foetida* in external morphology, while the divergence is progressive until in *myriocephala* one finds a highly specialized species with very numerous, small heads and many small fruits. The other eight chromosome species of this line are all closely related to *myriocephala* but are not so highly specialized through reduction in size of heads, flowers, and fruits. *C. lybica,* indeed, has the largest heads and fruits of the six species, although its chromosomes are the most like those of *myriocephala.* This may be explained, however, as the result of genic mutations unaccompanied by marked changes in chromosome morphology. In *C. hackeli* the evidence from external morphology is in fair agreement with the cytological evidence that this is a tetraploid or amphidiploid species.

Fig. 24. Phylogenetic chart of sixty-seven species of *Crepis.* The subgenus **Paleya,** *center,* is the most primitive. In the other three subgenera, **Barkhausia,** *upper right;* **Catonia,** *upper left;* and **Eucrepis,** *lower half,* the degree of relationship is roughly indicated by connections or absence of connections with **Paleya.**

Ixeris graminea probably should not be included in *Crepis*. Although its achenes are more like those of **Barkhausia** than they are like those of the typical *Ixeris* of Cassini, yet in other details of external morphology it is certainly closer to *Ixeris* and *Lactuca* than to *Crepis*. The evidence regarding the chromosomes provides assistance at this point. Although the number happens to be 16, the chromosomes are very much smaller than in any species of **Barkhausia** and in size and appearance they closely resemble those of *C. bulbosa* and *C. japonica* which are mentioned under **Catonia** and **Eucrepis** respectively.

Catonia

Catonia has less obvious connection with **Paleya** than has **Barkhausia**, yet the evidence from external morphology as well as from chromosomes strongly indicates such an origin. The existence of one species of **Paleya** (*C. oligocephala* Sch. Bip.) with **Catonia**-like characters is especially significant. Unfortunately the chromosomes of this species have not been seen. **Catonia** includes slightly less than one-fourth of the species thus far investigated cytologically and these are all perennials of the Old World. They are distributed in restricted areas scattered throughout Europe, Asia, and northern Africa; the subgenus is of much wider distribution than **Barkhausia**. All of these species have achenes resembling those of *C. oligocephala* more or less, but some of them are sufficiently different in their achenes and in other characters to necessitate the assumption of more than one prototype. Two prineipal lines are indicated in the chart, therefore, also two minor groups in each of which only one species has been examined cytologically.

Crepis sibirica exhibits closest resemblance to *C. oligocephala* in external morphology and the other species of this line are progressively distinct from the supposed prototype. The second group, *aurea*, *hookeriana*, and *bungei*, are so distinct from *C. oligocephala* as to necessitate the assumption that they arose from some other species. *C. tingitana*, on the other hand, resembles *aurea* in certain respects although very distinct in others; it does not seem improbable that the two arose from a common prototype. *C. paludosa* resembles *sibirica* and its allies in habit and leaves but the much smaller heads, and especially the very distinct achenes, make it necessary to assume a separate origin for *paludosa*.

Crepis bulbosa has long been recognized as one of the most outstanding species of the genus. In fact it has been referred to five

other genera, including *Aetheorhiza* of Cassini, who treated it as a monotypic genus. It is the only species of *Crepis* thus far examined having 18 chromosomes, and, as in *Ixeris graminea,* the chromosomes are very small. These facts would appear to warrant the reinstatement of Cassini's genus.

Eucrepis

These species not only show the least morphological resemblance to those of **Paleya** but they also comprise the most heterogeneous of the four subgenera. There is general resemblance within the subgenus, however, in the more numerous and smaller heads, the marked reduction of the outer involucral bracts, and the mostly smaller, beakless achenes. Of the thirty-eight species thus far studied cytologically, about one-third are annuals or biennials and two-thirds, perennials. This subgenus is the most widespread in geographic distribution, being represented in North America as well as throughout the Old World north of the equator. As is indicated in the chart, there are eight groups of obviously related species and some half-dozen species which are distinct from each other and from the several groups.

Crepis leontodontoides and *C. multicaulis* are sufficiently similar to the **Catonia** species, *tingitana* and *aurea,* to suggest a common origin. The geographic distribution of three of these species is not inconsistent with such a view. *C. multicaulis,* however, is widely separated from the other three geographically. At the same time it is among the most outstanding species in the genus because of extreme reduction in size of inflorescence although it is perennial like the other three. It seems probable, therefore, that *multicaulis* sprang from the same ancestral stock as the other three but is a more recent species and that there were several connecting forms which have disappeared.

The two annuals, *parviflora* and *capillaris,* are obviously close in external morphology and occupy different adjacent geographic areas. On the basis of specialization through reduction in size of flowers and fruits *parviflora* seems to be more recent and this view would be consistent with the chromosomal evidence if fragmentation of one of the *capillaris* chromosomes and marked changes in the others could be assumed. Fairly close to these are two other annuals, *neglecta* and *tectorum,* yet both are so different in their chromosomes as to require the hypothesis of a separate origin from each other and from the *capillaris* group. Both *tectorum* and *neglecta* exhibit a marked tendency to the production of a beak on the achene, but this is true also in certain forms of *leontodontoides.* It would appear that these

are really intermediate between **Eucrepis** and **Barkhausia** and that in course of time they may develop definitely beaked achenes.

Another group includes *nicaeensis*, which is found to be either annual or biennial, and *biennis*, which is usually biennial but sometimes blooms the first year. The close resemblance of the two species has been emphasized by Bischoff (1851), yet one has 8 chromosomes of medium size and the other about 40 rather smaller ones. It was deemed necessary to assume a common ancestral form with 10 chromosomes because of the evidence from interspecific hybrids (Collins and Mann, 1923; Collins, Hollingshead, and Avery, 1929) that *C. biennis* is an octoploid species. *Crepis ciliata* may also have derived its large number of chromosomes through polyploidy, but morphologically it is too distinct from *biennis* and *nicaeensis* to warrant the assumption of a very recent connection.

Crepis tenuifolia is a very outstanding species of **Eucrepis** not only because of its peculiarities of external morphology but also on account of its odd number of chromosomes discussed above. The fact that it appears to produce seed apomictically suggests the possibility that it originated as a hybrid between two species with 14 and 16 chromosomes respectively, although, as has been pointed out, the shapes of the various chromosomes offer no good evidence for this method of origin.

The four species with 12 chromosomes are very distinct from one another, but have quite similar heads, flowers, and fruits, and they are all perennials. *C. mollis*, with its nearly entire leaves and few, rather large heads, appears to be the least specialized; the other three are about equally advanced and are correspondingly less widely distributed.

C. nana and *elegans* form a unique group in external morphology, in geographic distribution, and in the number of their chromosomes. *C. nana* is the most widely distributed species in the genus. It occurs sporadically from Turkestan to northeastern Siberia and in North America from western Alaska to northwestern Canada, in Labrador, the Rocky Mountains, and the Sierra Nevada. *C. elegans* occurs in Alaska and the Rocky Mountains. There is good morphological evidence that *elegans* has been derived from *nana* and the extensive boreal and alpine distribution of *nana* indicates that it is either a much older species or a more successful species, perhaps both. There are no close relatives among the other species which have been examined cytologically.

Of the six species, *reuteriana*, *praemorsa*, *incarnata*, *gymnopus*, *pulchra*, and *palaestina*, the first four are perennials and the other two annuals. *C. praemorsa* and *C. incarnata* are very closely related although fairly distinct from each other morphologically, and still more distinct from their near relative, *gymnopus*. Similarly *pulchra* and *palaestina* are obviously related although still more distinct from each other. *C. praemorsa*, *incarnata*, and *gymnopus* bear less resemblance to *reuteriana*, however, than do *palaestina* and *pulchra;* they probably diverged from the *reuteriana* line considerably earlier than did *palaestina* and *pulchra*. Of the last two, *pulchra* is more highly specialized through reduction in size of flowers and its high self-fertility.

Crepis pannonica, *lacera*, and *chondrilloides* are obviously closely related perennial species and they probably stand in the above order in their phylogenetic relations to one another. This is indicated by differences in degree of dissection of the leaves. In *pannonica* the leaves are nearly entire; in *lacera* they are deeply dissected; while in *chondrilloides* they are extremely finely dissected. The geographic distribution is in agreement with this relation, since *pannonica* occurs from Hungary to Turkestan, *lacera* occurs only in central and southern Italy, and *chondrilloides* is restricted to a small region in Istria.

Crepis incana represents a group of perennial species which is closely related to the foregoing although very distinct. It was probably derived from the same ancestral stock.

Crepis dioscoridis bears the evidence of its relationship to *C. aspera* (of **Barkhausia**) in its peculiar marginal achenes and annual habit. If it arose from the same stock as *aspera* it must have diverged at a rather remote time. It is possible, of course, that this similarity in the marginal achenes is merely a case of parallel variation but if such is the case the ancestry of *dioscoridis* is still more obscure. Although it bears some resemblance to the *pannonica* group, especially in appearance of the involucre and in the morphology of its chromosomes yet in most respects it is very distinct from those species.

Pterotheca sancta seems to belong in *Crepis*, not only on the basis of its somatic chromosomes, but also on morphological grounds, the details of which cannot be discussed here. The origin of this species, however, is quite as uncertain as that of *dioscoridis* or *tenuifolia*. Its possible derivation from the **Barkhausia** stock is suggested by the resemblance of its chromosomes, but morphologically it seems quite as probable that it had a common progenitor with the *reuteriana* group.

The American species which have been examined cytologically, excepting *elegans* and *nana*, comprise a unique group with a different basic chromosome number ($n = 11$) from any other *Crepis*. None of them occurs east of the Mississippi River and the center of distribution is in southwestern Canada and northwestern United States. This suggests the probability of an Asiatic origin, but thus far no oriental species has been found with $n = 11$ chromosomes. Neither have any oriental species been found which closely resemble any of these American species. A few Asiatic species are known, however, which resemble certain American species in some ways and it may be shown eventually that they arose from a common prototype.

Although the problem of the phylogenetic relation of these American species to other **Eucrepis** is unsolved, certain assumptions may be warranted on the basis of chromosome numbers, external morphology, and ecology. All nine species are perennials. Three of them, *runcinata*, *glauca*, and *andersoni*, occur in moist meadows and alkali bogs and have fleshy rootstocks. The other six occur mostly in dry, rocky or gravelly places and have very long, slender, woody rootstocks. The first three are equally diverse from the other six in leaves, heads, and achenes. Thus there are two very different subgroups of American species and the situations with regard to chromosome numbers are equally diverse. Although fourteen different forms of *runcinata*, *glauca*, and *andersoni* have been examined, they all have $2n = 22$ chromosomes. But among the other six species, both tetraploidy and octoploidy occur as well as unbalanced polyploidy (33 and 55) accompanied by seed-bearing, which suggests reproduction by some form of apomixis. The existence of two such diverse groups in the same general region and with a common basic chromosome number suggests a common origin but divergence must have occurred at a comparatively remote period. Yet as compared with the Old World species of **Eucrepis**, these nine are probably of relatively recent origin. This would necessarily be the case if they were derived from Asiatic ancestors and it is strongly indicated by the higher chromosome numbers of this group. The probable method of origin of these remarkable groups of species is that first suggested by Winge (1917) and later confirmed experimentally by Clausen and Goodspeed (1925). This method consists of interspecific hybridization followed by delayed mitosis in the fertilized egg cell or in some initial cell of a shoot, during which the chromosomes all divide without passing to the poles. Thus a complete diploid set of chromosomes from

both parents is provided after which mitosis proceeds regularly. Some such amphidiploid hybrids are known to be vigorous and fully fertile. It is only necessary to assume natural crossing between two species with $n = 7$ and $n = 4$ chromosomes, followed by amphidiploidy, to explain the origin of species with 22 chromosomes. Because of the diversity between the two groups of American species, however, it seems necessary to assume that at least three different species were involved in the original crosses. Some of the other numbers which occur in the **Eucrepis** series may also have originated through amphidiploidy.

Crepis japonica (*Youngia lyrata* Cass.) is the type species of Cassini's genus. As in the case of *Ixeris graminea* and *Aetheorhiza bulbosa*, the chromosomes are much smaller than *Crepis* chromosomes. This evidence, together with that from external morphology and geographic distribution, will probably be considered sufficient to warrant the reinstatement of Cassini's *Youngia* as that genus was originally defined.

Summarizing briefly with respect to subgeneric relationship, **Paleya** is a small group of species which appear to be more primitive than all other *Crepis* at least in certain characters. There are two distinct subgroups of **Paleya**, viz., species with **Barkhausia**-like achenes and one species with **Catonia**-like achenes. **Barkhausia** contains species which show strong resemblance to certain **Paleya** species, although certainly more highly specialized. At the same time, within **Barkhausia** are found the highest degree of specialized structure in the beaked achenes and the largest amount of adaptation through development of the annual habit. The combination of these two lines of specialization, however, while advantageous in particular environments, has not resulted in wide distribution of the subgenus as a whole. This restriction of adaptation accompanying marked specialization must be considered along with the evidence that many species of **Barkhausia** appear to be of recent development. In **Catonia** is found a group of perennial species some of which exhibit evidence of relationship with an existing species of **Paleya** while for others it is necessary to assume other prototypes. The species of **Catonia** are less highly specialized than those of **Barkhausia** and **Eucrepis**, and most of the species are of comparatively restricted distribution. **Eucrepis**, the largest, most widely distributed, and most heterogeneous division, exhibits connections with both **Barkhausia** and **Catonia** in certain of its species but there is no evidence, among the species dis-

cussed in this paper, of close connection with **Paleya**. It seems most probable that the prototypes of **Eucrepis** and the present or earlier species of **Paleya** arose from a common stock subsequent to its differentiation from closely related genera such as *Hieracium* and *Lactuca*.

CHROMOSOMES AND PHYLOGENY

The cytologist or geneticist cannot fail to have noticed in the literature of recent years an increasingly close relationship between the study of the chromosomes and of external morphology with a view to classification. The impression is rather strong that in most cases it is the cytologist or the geneticist who has realized how useful or in some cases how fundamental his findings are to the elucidation of phylogenetic problems, and so has been led by a combined study of chromosomes and external morphology to formulate classification systems and phylogenetic hypotheses or to criticize those based on external morphology alone. It is to be hoped that taxonomists will come to the same realization and that in the future it will be considered as desirable to know the nature of the chromosomes of any plant as it is to be familiar with the details of its external morphology, particularly in cases where critical decisions are necessary.

Among the most outstanding cases where a knowledge of chromosome numbers has been useful in classification is that of the genus *Rosa*. Hurst (1925) utilized the cytological findings of Täckholm (1920, 1922) and Blackburn and Harrison (1921) in the classification of this genus, which in spite of the life-long labors of several botanists was still in an admittedly unsatisfactory state. These investigations had shown that there was in the genus a multiple series of chromosome numbers with a base number of seven. With this in mind a workable system was formulated, the most outstanding feature of which was that the whole *Caninae* section was characterized at reduction division by a condition often seen in hybrids, viz., the presence of univalent as well as bivalent chromosomes.

Quite different but equally interesting results were obtained by Heilborn (1924) in *Carex*. When the chromosome numbers were arranged according to the taxonomic relationship within the genus groups of adjacent numbers were found, nearly related species having numbers of about the same magnitude. In the genus *Triticum* a remarkable agreement in classifications based on morphology, resistance to disease, serological reactions, and chromosome numbers is

evident (Sax, 1921, 1923). Clausen (1927) found that *Viola* species of the same systematic subgroup belonged as a rule to the same series of chromosome numbers and in the *Melanium* section of the genus he made a new subdivision on the basis of chromosome numbers. He believes his investigations afford further proof of the great importance of cytology as an aid to taxonomic research.

It is the intention of the writers to do no more than point out a few of the many instances in which a knowledge of chromosome numbers has either aided in the making of a classification system or has added weight to one already made. It is true that in some instances a study of chromosome numbers has not helped greatly in classification, for species widely different morphologically may have the same chromosome number, as in *Crepis*. When such is the case this study has shown that a knowledge of the morphology of the chromosomes may be very illuminating. The chromosome number 8 occurs in thirty-two out of the seventy species discussed and in three of the four subgenera. The possibility is good that it occurs also in **Paleya**. But a comparative study of chromosome morphology has shown that these species with the same chromosome number are usually characterized by very different chromosomes.

A study of chromosome number and morphology in relation to classification was carried out by Sveshnikova (1927) in thirty species of *Vicia*. Three main groups—**Ervum** with 14 chromosomes in all species, **Cracca** with 12, 14, 24, and 28, and **Euvicia** with 12 and 14—were represented in the study. The chromosomes were divided into four groups according to the relative lengths of the arms and the presence of satellites and each species was described on this basis. When the species were arranged in groups according to the numbers of chromosomes of different classes, the classification was in general agreement with that usually applied by systematists. Indeed this investigator was able to make a key based on chromosome number and morphology which corresponded very nearly with one worked out by Ascherson on external morphology.

Wexelsen (1928), however, found no such parallelism in the differentiation of chromosome complexes and external morphology in his studies on chromosome numbers and morphology in eighteen species of *Trifolium*. Species which were far removed taxonomically and very different in morphology had very similar chromosome complexes, and very nearly related species had very different complexes. This he believes presents a very clear demonstration of parallel vari-

ation, for example the presence of one pair of satellited chromosomes in many species would be due to independent parallel mutations and not to the fact that they have been derived from a common source.

In most instances in Crepis similarity of chromosomes is most certainly associated with a common phylogenetic origin, although it may be necessary in one outstanding case at least to assume parallel variation to account for the similarity of the chromosomes of species far removed phylogenetically. We refer to the resemblance of the chromosomes of the *conyzaefolia*, *chrysantha*, *burejensis* group of **Catonia** to those of the *pannonica*, *lacera*, *chondrilloides* group of **Eucrepis.**

It is interesting to note what kinds of changes with respect to chromosome number and morphology the phylogenetic chart in figure 24 involves. The first difficulty we are faced with is the fact that only one species of the subgenus **Paleya,** which is believed to contain or to have contained the progenitors of the species of the other subgenera, has been examined cytologically. It seems probable that, since each of the other subgenera shows variation between species in the number of chromosomes, the same would be found to occur here. For the two lines (one in **Barkhausia,** one in **Catonia**), however, where the connection with **Paleya** is clearest ten is apparently the most primitive number. In each line one or more reductions to eight have occurred. This is true also of the second main line of **Catonia.**

The 8-chromosome species of **Eucrepis** could be assumed to have arisen from 8-chromosome **Paleya** species not examined cytologically or now extinct. If so it is necessary to assume that within **Paleya** a reduction from 10 to 8 or an increase from 8 to 10 chromosomes has occurred during the evolution of the species of this subgenus. Within **Eucrepis** the relations depicted in the chart (fig. 24) involve a reduction to 8 from the supposed 10-chromosome progenitor of *nicaeensis* and possibly a reduction to 6 from an 8-chromosome progenitor of *capillaris.*

The two known methods by which a reduction in number of chromosomes may take place are (1) the elimination of a pair of chromosomes following irregularities in meiosis and (2) the fusion of nonhomologous chromosomes. Examples are known where plants possess one pair of chromosomes less than the normal diploid set as in *Triticum* (Kihara, 1924, 1925), *Avena* (Huskins, 1927), and *Primula kewensis* (Newton and Pellew, 1929), but the species in question are admittedly of polyploid origin and the plants are partly or wholly

sterile. In other genera where monosomic plants are known (for example, in *Datura* and *Nicotiana*), which would be expected to give progeny lacking one chromosome pair, such progeny have not been reported. Moreover, M. Navashin's extensive study (1926, 1929) which included several thousand plants of three species of *Crepis*, failed to find a plant with even one chromosome missing. In view of these facts the explanation of reduction in chromosome number by elimination of a pair is, to say the least, questionable.

Similarly, evidence is lacking in this genus that a decrease in number could have resulted from end to end fusion of non-homologous chromosomes. M. Navashin found no instance of it in his investigations and neither does a study of the chromosomes of the various species in which a reduction is supposed to have occurred show any evidence of such a process. To take an extreme case, the 8 chromosomes of *senecioides*, presumably derived from a 10-chromosome stock, are on the whole smaller than those of the supposed stock from which they have sprung and certainly no one of them is long enough to represent simply an end to end fusion of two chromosomes of the parental stock.

It has been suggested in the animal kingdom by Wilson (1925) and Painter (1925) and in the plant kingdom by Delaunay (1926) and favorably taken up by Jaretsky (1928) that the occurrence of small chromosomes in a complex may represent an intermediate step in the process of gradual diminution in the size of a chromosome which terminates with its disappearance. Rather small chromosomes are not rare in *Crepis* although none have been found as small as those which first prompted this hypothesis.

It is also theoretically possible, although not very probable in species having such low chromosome numbers, that such a reduction in number might result from hybridization between two 10-chromosome species. This necessitates the assumption that such hybrids occasionally produce functional gametes having only 4 instead of the normal 5 chromosomes. Self-fertilization in such a hybrid might rarely produce new stable forms having 8 chromosomes. Thus far the experimental evidence from interspecific hybrids is against such a hypothesis (Navashin, 1927; Hollingshead, 1930).

The phylogenetic chart involves as well the assumption of numerous instances of increase in chromosome number. In some of these cases, such as *hackelei*, *bungei* 2174, and *incana*, all with 16 chromosomes, each species is morphologically closely related to certain 8-

chromosome species. Such cases are readily explained by chromosome doubling. Perhaps in the case of *hackeli* (from external morphological evidence), and of *bungei* 2174 (from the fact that no more than two satellited chromosomes were seen) the doubling followed hybridization between two 8-chromosome species. It has been pointed out earlier that a similar explanation may account for the chromosome numbers of *biennis*, *ciliata*, and the American species with a base number of 11, and the same explanation might conceivably be applied to the origin of the species with 12 and 14 chromosomes. Such an explanation would involve the assumption that species with 6 chromosomes featured in the ancestry of each of the last two groups. This seems rather unlikely since the one species known which has 6 chromosomes is, judging by its external morphology, of comparatively recent origin. It seems more probable that they have arisen from species with lower chromosome numbers by some method other than one involving a doubling of all the chromosomes.

How to account for an increase in number of one or more pairs of chromosomes is another problem. In many instances the evidence from chromosome morphology, as pointed out by Navashin (1925), is not in accord with an explanation which supposes the simple duplication of a pair of chromosomes already present as a result of irregular meiotic behavior, as suggested by Rosenberg (1918, 1920), for many species in which an increase is supposed to have occurred show no two pairs morphologically alike. Moreover, although M. Navashin (1926) found trisomics rather frequently in two *Crepis* species he has never found tetrasomics in their progeny (unpublished data). It must be borne in mind, too, that experimental evidence has shown that the tetrasomics investigated up to the present, as in *Datura* (Blakeslee and Belling, 1924), *Avena* (Huskins, 1927), and *Triticum* (Huskins, 1928) are usually much less viable than normal diploid plants and even when equally viable as in *Nicotiana* (Clausen and Goodspeed, 1924) they do not breed true. In this connection, however, the occurrence of the numbers 10, 11, 12, and 13, with the variation probably involving only a single chromosome type, in apparently typical and quite viable plants of *C. alpina* var. *syriaca* is of great interest. One may assume that it will be possible to isolate constant 10-, 12-, and possibly even 14-chromosome races from this species. Whether the supernumerary chromosome is a relic of some hybrid ancestry, or whether it represents the phenomenon designated by M. Navashin as "novation," or whether it represents part of a normally 12-chromosome

complex are as yet matters of speculation only. Instances are known in the genus where a chromosome from one species has been added to the normal complex of another as a result of hybridization (Hollingshead, 1930) but the plants are weak and sterile. Similarly M. Navashin's plants which contained apparently new chromosomes of unknown origin were inviable and it has been pointed out above that plants lacking one pair of chromosomes (except in polyploid species) have not been found. Of the three suggested hypotheses to account for this situation in *syriaca*, the first (hybrid origin) appears to be the least improbable.

In some few instances the hypothesis of transverse segmentation can be advanced to account for increased chromosome number in this genus, as suggested by Mann (1925). This hypothesis is believed to account for an increased number of chromosomes in certain other genera, for example in *Secale* (Gotoh, 1924, and Belling, 1925) and in other cases (cf. Kuhn, 1928). M. Navashin (1926) found a *C. tectorum* plant in which one chromosome had fragmented and each part behaved as a new chromosome in mitosis. This process has been suggested (above) as having played a part in the evolution of *C. parviflora* from *capillaris*. Such a hypothesis, however, while explaining adequately chromosome lengths, fails to take into account differences in the shapes of the various chromosomes and must even in this instance have been accompanied or followed by changes in position of spindle-fiber attachment constrictions, which will be discussed later.

In addition to changes involving increase and decrease in number of chromosomes, the chart necessitates the assumption that changes in chromosome size have occurred during the evolution of the various species. In *Muscari*, Delaunay (1926) came to the conclusion that diminution in chromosome length by a slow process called by him "historiation" had occurred in the evolution of the chromosomes of the species he studied. Jaretsky (1928) favors the same process as a mode of chromosome evolution from his studies on POLYGONACEAE. Heitz (1928) recognizes changes in length of chromosomes as of fundamental importance in the evolution of chromosomes. Sveshnikova (1927) concluded that in *Vicia*, among the processes which had occurred during the evolution of the species she studied, there had been a reduction of chromatin connected with variation in external morphological features.

This study would seem to show that both increase and decrease in chromosome size have been relatively frequent occurrences in the evolution of the various species of the genus *Crepis*. Morphologically similar species usually have similar chromosomes and it is only within such closely related groups that it is safe to assume which chromosomes are descended from a common ancestor. In the *vesicaria*, *lybica*, etc., group, which have very similar chromosome complexes, it is possible to pick out *lybica* by the uniformly slightly larger size of its chromosomes. In this connection it is worth noting that Wexelsen found two varieties of *Trifolium repens* to have chromosomes of different size, one having uniformly larger chromosomes than the other. Though it is true that, generally speaking, the various *Crepis* species have "large" or "small" chromosomes, it does not follow that increase or decrease in length has similarly affected all chromosomes in a complex. This is obvious from a glance at such a complex as that of *setosa* which contains a very short pair along with comparatively long pairs of chromosomes. The evidence from *bursifolia-aspera* hybrids (Babcock and Clausen, 1929) indicates that the satellited chromosomes of these species are homologous. Most of the chromosomes in the two species are of the same size order but in this particular chromosome pair the species differ very markedly, *aspera* having long, and *bursifolia* unusually short, satellited chromosomes.

As has been noted earlier, cross-division of chromosomes is not unknown in the genus and as M. Navashin (1926) has pointed out, such a process might be followed by elimination of part of the fragmented chromosome. Such an occurrence could be supposed to account for the difference in size between apparently homologous chromosomes of different species were it not that no evidence is available to show that such a loss can take place and the individual still survive. Further, it has been shown that several authors favor a gradual change in chromosome size as the way in which chromosomes in related species come to differ from each other. Navashin (1926) pointed out that differences in satellite size between races of a single species may illustrate this kind of change and stated that the origin of new distinct species could probably be explained by the continual addition of such small changes. The fact that chromosomes of all sizes intermediate between largest and smallest are to be found in this genus would seem to offer good evidence for this theory.

Lastly, any evolutionary hypothesis must take into account changes in chromosome shape which are largely determined by the

presence or absence of satellites and the position of the spindle-fiber attachment. In this connection cases in which homologous chromosomes are different (heteromorphic pairs) are instructive. They would seem to offer evidence that rare changes in chromosome shape may occur without markedly affecting the external morphology.

Size differences in satellites on homologous chromosomes have been reported by a number of investigators (cf. Kuhn, 1928). In *Crepis*, M. Navashin found races of *C. dioscoridis* with two large satellites, with two small satellites, and with one large and one small satellite. In *Rumex scutatus*, Jaretsky found some plants in which one of the chromosomes of a pair have satellites and others in which there were no satellites at all. Such a condition could be expected to lead to a race with both members of the pair bearing satellites. The significance of such findings for evolution of chromosomes of a different type is obvious.

Heteromorphism, which involves a difference in position of spindle-fiber attachment, is well known in the animal kingdom. In plants, in addition to the instances of sex chromosomes which may differ both in size and shape, a few cases of heteromorphic autosomes have been found. In different samples of both *Vicia angustifolia* and *V. sativa*, Sveshnikova (1927) found the same chromosomes showing slightly different ratios in arm length. Two cases of heteromorphic pairs are reported in this paper, viz., *Pterotheca sancta* and *Crepis pulchra*. The case of *C. pulchra* is particularly interesting for here plants with two chromosomes of each kind and one with one of each were found. The first two of these races could, conceivably, if isolated, develop in the course of time into different species each characterized by its particular chromosomes.

Heitz (1928) holds that the primitive chromosome form is the equi-armed one and that asymmetrical shortening (or lengthening) gives rise to chromosomes with unequal arms. Equi-armed chromosomes occur in each subgenus and in many species of *Crepis*. Usually they are the smaller chromosomes of the complex, although they may be the largest as in the *pulchra*, *palaestina*, etc., group. There is no consistent evidence in *Crepis* to support Heitz's theory that such chromosomes are more primitive, for although they do occur perhaps more frequently in some of the supposedly older species (*C. asturica*, *C. foetida*) with low numbers, yet they also occur in the highly specialized *C. senecioides*.

Heitz's theory would also imply that a change in the form of a chromosome results only from a change in length of one of the arms. Sveshnikova does not state whether the chromosomes which showed different ratios of arm length in her material were the same length or not. In the cases observed by the writers, however, the heteromorphic pairs were nearly or quite the same length and it seems more probable that the change in form has resulted from a shifting of the attachment constriction rather than from a lengthening of one arm and a shortening of the other.

Summarizing, the following changes in chromosome numbers must be assumed to have occurred during the evolution of these sixty-seven species of *Crepis*, if the phylogenetic grouping proposed here be accepted. (1) Reduction in number from 10 to 8 and from 8 to 6, changes which it is difficult to explain in the light of our present knowledge. It is possible, however, that such changes might have come about through a process of gradual diminution of a particular pair of chromosomes or that interspecific hybridization or fusion of nonhomologous chromosomes might have given rise to a new species with the reduced number, although there is no experimental evidence for such hypotheses. (2) Increase in number from 8 to 16, a change which may have occurred in either of two ways, viz., doubling of the $2n$ group resulting in true tetraploidy; and doubling in a hybrid between two 8-chromosome species, resulting in amphidiploidy. (3) Increase from 10 to 40 or thereabouts (*biennis, ciliata?*) which according to experimental evidence must have resulted from once repeated doubling of the $2n$ group producing octoploidy. (4) Increase from 22 to 33, 44, 55, and 88. The even numbers probably arose through chromosome doubling as described above and the odd ones may have arisen through hybridization between even numbered forms or by the fusion of somatic gametes with normal ones. (5) Increase from lower numbers to 12, 14, 15, and 22 chromosomes, which in some cases may have resulted from transverse segmentation. The higher even numbers could be explained by the assumption of amphidiploidy and the odd one could conceivably have arisen as a result of hybridization, though again experimental evidence for such an origin is lacking. In addition to changes in number many changes in chromosome size apparently have occurred and to the present writers it seems probable that most of these changes have taken place gradually during the phylogenetic differentiation of the species. Lastly there have been many changes in chromosome shape, and the occurrence of races

within a species which differ in the shape of one chromosome pair and of plants with heteromorphic chromosome pairs indicates that this is not a very uncommon occurrence in phylogeny.

On the whole it seems probable that a number of different mechanical processes affecting chromosome organization have played a part in the evolution of chromosomes in this genus. Processes such as fragmentation, union, inversion, deletion, translocation, and duplication have occurred in *Drosophila*. Painter and Muller (1929) and Muller and Painter (1929) have recently described changes in chromosome shape resulting from such processes actually induced by irradiation with X-rays. These studies are extremely significant in connection with problems of chromosomes and phylogeny, for such processes can account for changes in size and shape and increase and decrease in number of chromosomes. In particular they offer a possible explanation for the 6, 8, 12 portion of the *Crepis* chromosome series whose manner of origin from a supposed 10-chromosome ancestor presents the most difficult problem in the study of the evolution of chromosomes within the genus.

SUMMARY AND CONCLUSIONS

The number and morphology of the somatic chromosomes of seventy species (including three which have been considered *Crepis* but will probably be assigned to other genera) were investigated in connection with a taxonomic study of the genus. The study of chromosome morphology has increased materially the value of the cytological findings in connection with classification.

Size differences, the occurrence of satellites, and shape as determined by spindle-fiber attachment were used to distinguish the various chromosomes.

The species discussed include twenty-seven whose chromosome numbers have not previously been counted and a number which have not been figured previously. A drawing showing a somatic metaphase which depicts as far as possible details of morphology is included for each species. The known series of chromosome numbers of Old World species is 6, 8, 10, 12, 14, 15, 16, and 40±. That of the American species is 14, 22, 33, 44, 55?, and 88?. Without doubt these latter numbers are members of a polyploid series, as are some of the numbers in the Old World group. Others probably originated through interspecific hybridization. There is considerable evidence pointing

to 10 as the basic number. An alternative hypothesis is the assumption that 8 is the more primitive number in *Crepis*. No evidence exists at present to support this assumption.

In regard to size of chromosomes, there is a range of sizes, the extremes of which may be roughly expressed by the ratio 1:2. It should be noted, however, that the species having the smallest chromosomes (*senecioides*, *nana*, *elegans*, and *leontodontoides*) comprise only a small fraction of the entire number of *Crepis* species thus far studied. In comparison with these the chromosomes of the remaining species may be designated as medium, medium-large, and large, but within each of these categories there is considerable variation so that the entire list of species could be arranged in a nearly continuous series on the basis of chromosome size. Species representing the extremes in size differences occur in **Eucrepis**, while **Barkhausia** contains one species having chromosomes of the smallest size, and **Catonia** has several species with very large chromosomes. The variation in chromosome sizes, therefore, is not peculiar to any one subgenus; on the contrary it is distributed throughout the genus.

With regard to shape of the chromosomes, while there are many minor differences between individual species, there is a general similarity in all the species. Occurrence of satellites and position of constrictions are the most useful differences in shape. The occurrence of at least one pair of satellited chromosomes is practically constant throughout all the species. About one-third of the species have at least one pair of chromosomes with approximately median constrictions. In all other chromosomes the constrictions are located at some point nearer the proximal end of the chromosome.

A chart was drawn up to show the four major subdivisions of the genus and the chromosome numbers of the species discussed. This chart depicts the phylogenetic groups which were worked out by combining data on chromosome number and morphology with evidence from external morphology, consideration having been given to geographic distribution and evidence from interspecific hybridization. The chromosomes of the species in the various phylogenetic groups were discussed and their resemblances and differences noted.

In **Paleya**, considered the most primitive subgenus and supposed to contain or to have contained the progenitors of the other subgenera, only one species has been examined and it has 10 chromosomes. Probably further study would discover other chromosome numbers in this section. The subgenus **Barkhausia** contains species with 8, 10, and 16

chromosomes, and these same numbers and one 12-chromosome species are found in **Catonia**. **Eucrepis,** the largest subgenus, contains the greatest number of species and those whose connection with **Paleya** is least obvious. The numbers 6, 8, 10, 12, 14, 16, and 40 are found in the Old World species of the subgenus. With the exception of two closely related species, one of which also occurs in the Old World, the American species form a polyploid series with a base number of 11. These facts, together with the heterogeneity of **Eucrepis,** lead to the inference that this subgenus consists of a number of related phylogenetic lines and that the earlier connecting forms and the more primitive ancestors have all disappeared. Several of these diverse subgroups under **Eucrepis** are represented among the species thus far studied by individual species while others contain from two to six species which are obviously closely related both from their external morphology and their very similar chromosomes.

Two instances of heteromorphic chromosome pairs involving differences in point of spindle-fiber attachment were found (*C. pulchra* and *Pterotheca sancta*) and in the former species, in addition to the plant showing this condition, other plants with a pair of each of the different chromosomes were found. A difference in size of satellites on homologous chromosomes was noted in *C. foetida.*

In one case (*C. alpina* var. *syriaca*) variation in chromosome number from 10 to 13 was found and the variation appeared to involve one particular chromosome type.

The phylogenetic system proposed involves the assumption of several different kinds of chromosome changes. They include increase and decrease in chromosome number and increase and decrease in size and change in shape. Ways in which these changes may have come about are discussed and the most likely ones are pointed out.

In general, in each section of the genus, morphologically similar species have similar chromosomes and the writers are more firmly convinced by this investigation of the value of such a study of chromosomes in relation to taxonomy. Certainly there is a fairly close parallelism in *Crepis* between number and morphology of the chromosomes and phylogenetic relationship.

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